EGG CAPSULES OF DEEP-SEA CATSHARKS FROM EASTERN NORTH ATLANTIC, WITH FIRST DESCRIPTIONS OF THE CAPSULE OF *GALEUS MURINUS* AND *APRISTURUS APHYODES* (CHONDRICHTHYES: SCYLIORHINIDAE)

by

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ABSTRACT. - Egg capsules of four species of the deepwater catshark genera *Galeus* and *Apristurus* are described and compared. The egg capsules of *G. murinus* and *A. aphyodes* are firstly described from 4 and 9 capsules respectively, collected in the mother's oviducts. Unlike numerous species of the family, their egg capsules do not have prolonged tendrils. The smallest gravid females of *G. murinus* and *A. aphyodes* measure 460 and 490 mm respectively. Their oviparous mode of reproduction was confirmed. There is only one egg capsule per oviduct for both species, indicating they are single oviparous species. Comments are made on the oviparity of the catsharks of these genera.

RÉSUMÉ. - Les capsules ovigères des Scyliorhinidae de profondeur de l'Atlantique Nord-Est, avec la première description des capsules de *Galeus murinus* et *Apristurus aphyodes* (Chondrichtyens, Scyliorhinidae).

Les capsules ovigères de quatre espèces de Scyliorhinidae de profondeur des genres *Galeus* et *Apristurus* sont décrites et comparées. Les capsules ovigères de *G. murinus* et *A. aphyodes* sont décrites pour la première fois, respectivement à partir de 4 et 9 capsules prélevées dans les oviductes des mères. Contrairement à de nombreuses espèces de la famille, leurs capsules ovigères ne sont pas prolongées par des vrilles. Les plus petites femelles gravides de *G. murinus* et d'*A. aphyodes* mesurent respectivement 460 et 490 mm. L'oviparité de ces roussettes a été confirmée. Il n'y a qu'une seule capsule ovigère par oviducte pour chacune de ces espèces, ce qui indique une reproduction de type simple oviparité. L'oviparité des roussettes appartenant à ces genres est commentée.

Key words. - Scyliorhinidae - *Galeus murinus* - *G. melastomus* - *Apristurus aphyodes* - *A. laurussonii* - ENA - Egg capsule - Oviparity.

In the eastern North Atlantic Ocean and the Mediterranean Sea, three species of *Galeus* occur: *G. melastomus* Rafinesque, 1810, *G. atlanticus* (Vaillant, 1888) and *G. murinus* (Collett, 1904). Descriptions of the egg capsules of *G. melastomus* are given by Tortonese (1956), Capapé and Zaouali (1977) and Cadenat and Blache (1981). Muñoz-Chápuli and Perez Ortega (1985) described egg capsules of *G. atlanticus*. However, there is no description of the egg capsule of *G. murinus*.

Five species of *Apristurus* are known from the eastern North Atlantic *i.e.*, *Apristurus laurussonii* (Saemundsson, 1922) (= *A. maderensis* Cadenat & Maul, 1966), *A. microps* (Gilchrist, 1922), *A. atlanticus* (Koefoed, 1927), *A. manis* (Springer, 1979), and *A. aphyodes* Nakaya & Stehmann, 1998. However, the egg capsule is not known for these species, except for *A. laurussonii* (Cadenat et Maul, 1966; Nakaya and Sato, 1998).

Egg capsules of *G. murinus* and *A. aphyodes* were obtained from commercial fisheries and are herein described for the first time, together with those of species of the genera from eastern North Atlantic, then the oviparity of the catsharks is discussed.

MATERIALS AND METHODS

The terminology of the egg capsule follows Cox (1963) and Gomes and De Carvalho (1995). The specimens examined were collected by commercial bottom trawlers. Specimens of *Galeus murinus* and *Apristurus aphyodes*, and theirs egg capsules are catalogued in the collections of the Muséum National d'Histoire Naturelle (MNHN) in Paris.

Specimens examined

Galeus murinus (4 egg capsules from 2 specimens). - 2 egg capsules from MNHN 2000-1734, female, 471 mm TL, 52°26'-52°38'N, 15°09'-15°06'W, 1100-1130 m, 20 Mar. 2000; 2 egg capsules from MNHN 2001-1049, female, 460 mm TL, 55°41'-55°54'N, 9°50'W, 900-950 m, 13 Mar. 2001.

Galeus melastomus (34 egg capsules from 9 speci-

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mens). - 2 egg capsules from 636 mm TL female, 56°N, 9°30'W, 1100 m, 1999; 3 egg capsules from 641 mm TL female, 56°N, 9°30'W, 1100 m, 1999; 2 egg capsules from 650 mm TL female, 56°N, 9°30'W, 1100 m, 1999; 1 egg capsule from 676 mm TL female, 59°40'N, 6°13'W, 235 m, 20 Jul. 1999; 11 egg capsules from 790 mm TL female, off British Isles, Dec. 1999; 4 egg capsules from 621 mm TL female, off British Isles, 2000; 6 egg capsules from 671 mm TL female, off British Isles, 2000; 2 egg capsules from 646 mm TL female, off British Isles, 2000; 3 egg capsules from 639 mm TL female, 57°05'N, 9°W, 400-420 m, Mar. 2001.

Apristurus aphyodes (9 egg capsules from 5 specimens). - 1 egg capsule from MNHN 1999-0792, female, 501 mm TL, 54°N, 13°30'W, 800 m, 25 May 1998; 2 egg capsules from female, Apr. 1999; 2 egg capsules from MNHN 2000-1735, female, 490 mm TL, 54°30'N, 11°W, 1300 m, 12-28 Jun. 1999; 2 egg capsules from MNHN 2000-1736, female, 509 mm TL, 59°13'N, 8°W, 1300 m, Jul. 1999; 2 egg capsules from MNHN 2000-1742, female, 525 mm TL, 54°20'-54°17'N, 19°45'-19°32'W, 1230-1249 m, 16 Mar. 2000.

Apristurus laurussonii (8 egg capsules from 4 specimens). - 2 egg capsules from 689 mm TL female, 56°30'N, 9°15'W, 1080 m, Aug. 1998; 2 egg capsules from 667 mm TL female, 53°54'-53°48'N, 13°43'-14°02'W, 1140-1159 m, 11 Mar. 2000; 2 egg capsules from 685 mm TL female, 54°30'N, 11°W, 1300 m, 19-28 Jun. 1999; 2 egg capsules from 681 mm TL female, 52°26'-52°38'N, 15°09'-15°06'W, 1100-1130 m, 20 Mar. 2000.

RESULTS

Detailed measurements and weights of the full egg capsules are given in table I.

Egg capsule of *G. murinus* (Fig. 1A) is small in size and relatively slender (54-56 mm in length and 14-17 mm in width); a weak neckline constriction is present at about one fifth of the length from the anterior end; surface of the capsule is completely covered by weak and fine fibrous tissue, giving a thick hairy appearance when submerged in the water; capsule is opaque because of its fibrous texture; anterior end is truncate, without any process; posterior end is rounded gently and possesses a single badly defined process, extending beyond the capsule; lateral edge is not developed; color is uniformly golden yellow. Only one egg capsule is found from each oviduct.

Egg capsule of *G. melastomus* (Fig. 1B) is slightly larger than those of *G. murinus* in size (51-65 mm in length

Table I. - Measurements (in mm) and weight (in g) of full egg capsules of *Galeus murinus*, *G. melastomus*, *Apristurus aphyodes* and *A. laurussonii*.

	Mothers			Egg capsules				
	Reference	TL	Weight	n	Length	Width	Depth	Weight
Galeus murinus	MNHN 2000-1734	471	373	2	54.5-55.5	14.5	11.5	3.4-3.5
	MNHN 2001-1049	460	391	2	55-56	17	9	2.5-2.7
Galeus melastomus	-	636	712	2	59	20	-	3.5
	-	641	762	3	56-60	18-21	8-10	3.0-4.9
	-	650	902	2	55-57	21	10	-
	-	676	852	1	60	22	-	4.2
	-	790	-	11	60.5-64.5	21-23	10.5-13	4.6-6.3
	-	621	657	4	-	-	-	-
	-	671	915	6	61.5-65	20-21	12-13	6.6-7.1
	-	646	732	2	51.3-53	19-19.5	11-11.5	5.2-5.6
	-	639	717	3	53-54.5	21	10-11	4.5-5.4
Apristurus aphyodes	MNHN 1999-0792	501	398	1	46	16	9	2.2
	-	-	-	2	49.5	14	10	3.5
	MNHN 2000-1735	490	458	2	42.5-43.5	15	8.5-9	1.8-2.0
	MNHN 2000-1736	509	494	2	47.5-48	16-16.5	8.5	2.9-3.1
	MNHN 2000-1742	525	593	2	51.5	16	9-9.5	3.1-3.4
Apristurus laurussonii	MMF 18750	668	-	2	68-72.3	24.6-26.5	-	-
	ISH 23-1981	622	-	2	62.6	-	-	-
	-	689	1198	2	72	24	9	-
	-	667	994	2	-	-	-	-
	-	685	1170	2	61-62	27	10	-
	-	681	1071	2	-	-	-	7.8-8.4

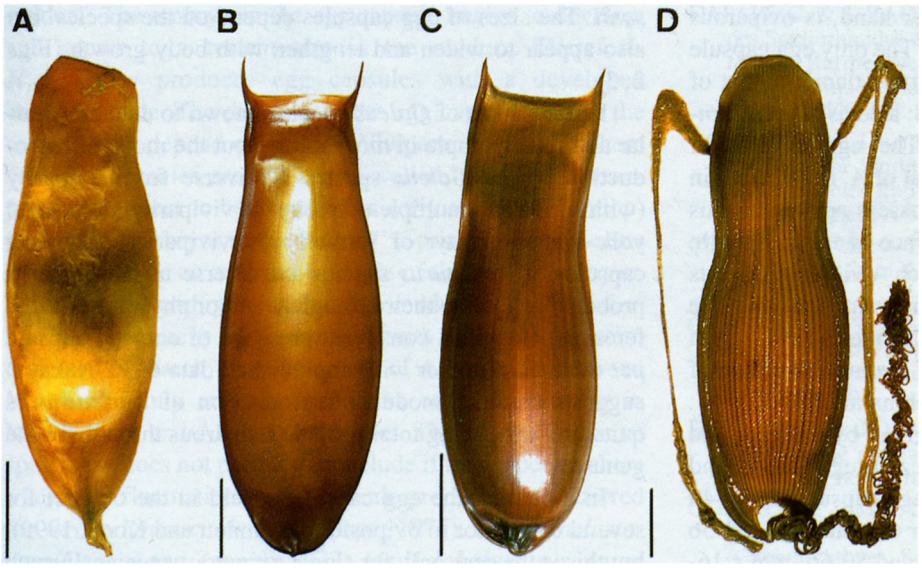

Fig. 1. - Egg capsules of *Galeus murinus* (**A**: MNHN 2000-1734, 54 mm in length); *G. melastomus* (**B**: uncatalogued, 60 mm); *Apristurus aphyodes* (**C**: MNHN 1999-0792, 46 mm) and *A. laurussonii* (**D**: uncatalogued, 68 mm). Scale bars = 10 mm.

and 18-23 mm in width) and is roughly vase-shaped, with posterior part oval in shape; a neckline constriction is present at about one fifth of the length from the anterior end; surface is smooth and glossy, keratin-like texture; capsule is moderately translucent; posterior end is rounded, with 2 very short coiled horns in close touch; anterior end of the capsule is truncate, with a small horn on each corner; lateral edge weakly flanged; four white respiratory fissures as grooves of 5-8 mm in length, two on each side (one anterior-left and one posterior-left) are present; color is golden brown when extracted from the oviduct, changing to dark brown after exposure to sea water. Each oviduct contained one to six egg capsules.

Egg capsule of *A. aphyodes* (Fig. 1C) is rather small in size (43-52 mm in length and 14-17 mm in width), and is roughly vase-shaped, with posterior part oval in shape; a neckline constriction is at about a third of the length from anterior end; surface is smooth and glossy, keratin-like texture; capsule is opaque, posterior end is rounded, with 2 very short coiled horns in close touch; anterior end of the capsule is truncate, with a short horn on each corner; late-ral edge is not developed; color is golden brown when extracted from the oviduct, changing to bronze brown after exposure to sea water. Only one egg capsule is found from each oviduct.

Egg capsule of *A. laurussonii* (Fig. 1D) is larger than that of *A. aphyodes* in size (61-72 mm in length and 24-27 mm in width); a neckline constriction is at about a third to two fifth of the length from the anterior end; surface is entirely covered by villus-like fibers forming 25 to 26 longitudinal striations; capsule is opaque because of its rough, suede texture; posterior end with two very long and tightly coiled tendrils; anterior end more or less rounded with long and weak fibrous thread one each corner; lateral edge flanged, forming keel-like ridge; color is bronze brown. Only one egg capsule is found from each oviduct.

DISCUSSION

All the described capsules were found in the posterior part of the oviducts, suggesting that all were completely formed and ready for oviposition. Because egg capsules within genera of Scyliorhinidae present an important variability in the shape, texture and ornamentation, they can be used as good taxonomic characters, specially in morphologically homogeneous genus like *Apristurus*.

Although the mode of reproduction of the members of the family Scyliorhinidae is generally oviparous, the genus *Galeus* is an exception, with both oviparous and viviparous species. *G. polli* from the Atlantic off southern Morocco to Namibia is a viviparous species (Poll, 1951; Cadenat, 1959). However, *G. melastomus* is oviparous, with up to 13 egg capsules in the oviducts at one time (multiple oviparity of Nakaya, 1975). According to Muñoz-Chápuli and Perez Ortega, (1985), *G. atlanticus* is also a multiple oviparous species, with at least 9 egg capsules in both oviducts. They described the egg capsules to be very similar in shape to, but smaller (38-40 mm in length and 11-13 mm in width) than that of *G. melastomus*. According to Compagno (1984), *G. murinus* grows maximally at least to 63 cm in total length, and Muñoz-Chápuli and Perez Ortega (1985) reported 479-545 mm TL male having fully calcified claspers, but almost nothing is known about its biology. Discovery of an egg capsule from each oviduct in 460 and 471 mm TL specimens indicates that *G. murinus* is a single oviparous species, same as *G. eastmani* and *G. nipponensis* from western North Pacific (Nakaya, 1975), and that the female of *G. murinus* are mature at 460 mm or less in total length.

The genus *Apristurus*, on the other hand, is oviparous throughout the genus, as far as known. The only egg capsule of *Apristurus* known from eastern North Atlantic is that of *A. laurussonii* (Nakaya and Sato, 1998; also as *A. maderensis* by Cadenat and Maul, 1966). The egg capsule of *A. aphyodes* is quite different from that of *A. laurussonii* in that the anterior and posterior ends possess neither fibrous tissues nor tendrils, and that the surface is quite smooth. Presence of an egg capsule in each oviduct suggests *A. aphyodes* also to be a single oviparous species. The smallest *A. aphyodes* containing egg capsules was 490 mm TL, and this coincides with the size of sexual maturation of the species, shown by Nakaya and Stehmann (1998).

Together with the measurements given by Cadenat and Maul (1966), Muñoz-Chápuli and Perez Ortega (1985), and Nakaya and Sato (1998), the sizes of egg capsule are 38-40 mm in length x 11-13 mm in width for *G. atlanticus*, 54-56 mm x 14-17 mm for *Galeus murinus*, and 50-66 mm x 16-23 mm for *G. melastomus*. The capsule sizes of *Apristurus* species are 43-52 mm in length x 14-17 mm in width for *A. aphyodes*, and 61-72 mm x 24-27 mm for *A. laurussonii*. The sizes of egg capsules depend on the species, but also appear to widen and lengthen with body growth (Figs 2, 3).

Egg capsules of *Galeus* species known to date are similar and rather simple in morphology, but the mode of reproduction of the *Galeus* species is diverse from oviparity (with single and multiple oviparity) to viviparity (aplacental yolk sac viviparity; or formerly ovoviviparity). The egg capsules of *Apristurus* species are diverse in morphology, probably reflecting their biological and/or phylogenetic differences. However, consistent presence of one egg capsule per oviduct (together with unpublished data of K. Nakaya) suggests that the mode of reproduction of *Apristurus* is quite uniform, being totally single oviparous throughout the genus.

In oviparity, the egg capsule is held in the oviduct for several days prior to oviposition (Hamlett and Koob, 1999), but this is the case only for single oviparous species. In such species of multiple oviparity as *Halaelurus buergeri*, the egg capsules are kept for several months in the oviduct, and this results in accumulation of multiple egg capsules in an

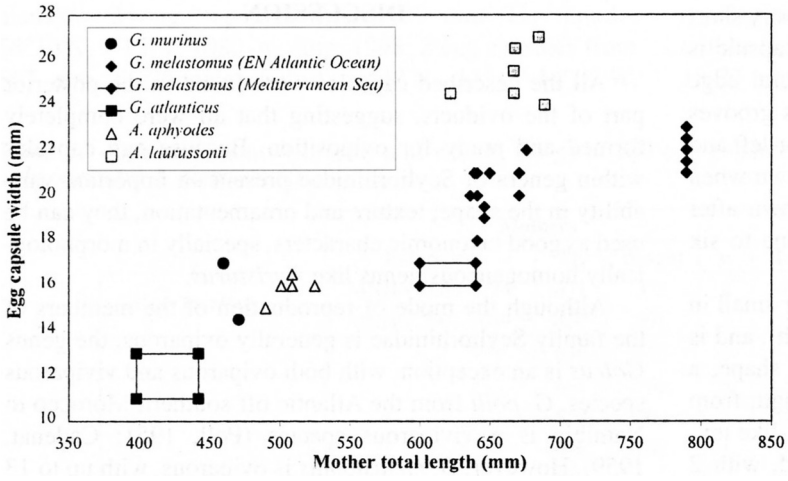

Fig. 2. - Egg capsule width in relation to mother total length for *Galeus murinus*, *G. melastomus*, *G. atlanticus*, *Apristurus aphyodes* and *A. laurussonii*. Data for *G. atlanticus* and *G. melastomus* (Mediterranean Sea) were taken from Muñoz-Chápuli and Perez Ortega (1985), and are shown as a range (square).

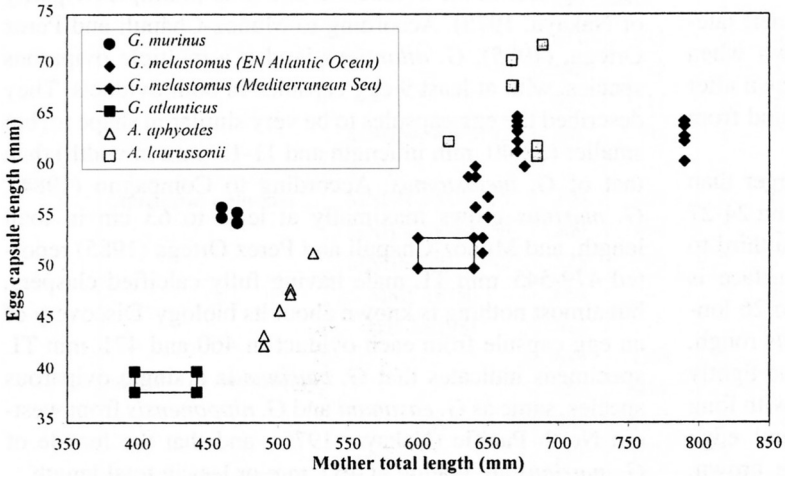

Fig. 3. - Egg capsule length in relation to mother total length for *Galeus murinus*, *G. melastomus*, *G. atlanticus*, *Apristurus aphyodes* and *A. laurussonii*. Data for *G. atlanticus* and *G. melastomus* (Mediterranean Sea) were taken from Muñoz-Chápuli and Perez Ortega (1985), and are shown as a range (square).

oviduct. The embryo in the egg capsule begins to develop, and grows to a certain size in the oviduct. Therefore, *H. buergeri* produces egg capsules with a developed embryo inside. The duration of the egg capsule kept in the oviduct may depend on species. Viviparous *G. polli*, where "the egg capsules are not heavy-walled, substantial structures and appear to be absorbed in early stages of development of the embryos in the oviduct" (Springer, 1979), seems in a sense to be an extreme example of the multiple oviparity, where the embryos hatch in the oviduct.

Two specimens of *G. murinus* with egg capsules were collected in March, five specimens of *A. aphyodes* between March and July and six specimens of *A. laurussonii* in March, June and August to October. The small number of specimens does not permit to conclude if these species show a seasonal fluctuation in egg capsule production as inferred for *Scyliorhinus canicula* (Capapé, 1977), for *G. melastomus* (Capapé and Zaouali, 1977), for *Holohalaelurus regani* (Richardson *et al*., 2000), and for *A. brunneus* and *Parmaturus xaniurus* (Cross, 1988).

As the oviparity is generally considered to be a primitive mode of reproduction in elasmobranch fishes (Dulvy and Reynolds, 1997), these facts mentioned above indicate that the genus *Galeus* is a reproductively more advanced member among the catsharks, that the multiple oviparity is to be an advanced style in the oviparity, and that the oviparous genus *Apristurus* is considered to be a primitive condition in the family.

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REFERENCES

CADENAT J., 1959. - Notes d'ichtyologie ouest-africaine. XX. - *Galeus polli* espèce nouvelle ovovivipare de Scyliorhinidae. *Bull. Inst. Fr. Afr. Noire*, Sér. A, 21: 395-409.

CADENAT J. & J. BLACHE, 1981. - Faune Tropicale XXI. Requins de Méditerranée et d'Atlantique (plus particulièrement de la Côte Occidentale d'Afrique). 330 p. Paris: ORSTOM.

CADENAT J. & G.E. MAUL, 1966. - Note d'ichtyologie ouest-africaine. 43. Description d'une espèce nouvelle du genre *Apristurus*, *Apristurus maderensis*. *Bull. Inst. Fond. Afr. Noire*, 28: 769-782.

CAPAPÉ C., 1977. - Contribution à la biologie des Scyliorhinidae des côtes tunisiennes. I. *Scyliorhinus canicula* (Linné, 1758): Répartition géographique et bathymétrique, sexualité, reproduction, fécondité. *Bull. Off. Natn. Pêch. Tunisie*, 1: 83-101.

CAPAPÉ C. & J. ZAOUALI, 1977. - Contribution à la biologie des Scyliorhinidae des côtes tunisiennes. VI. - *Galeus melastomus* Rafinesque, 1810. Répartition géographique et bathymétrique, sexualité, reproduction, fécondité. *Cah. Biol. Mar.*, 18: 449-463.

COMPAGNO L.J.V., 1984. - FAO Species Catalogue. Vol. 4, Sharks of the World. An annotated and illustrated Catalogue of Shark Species known to Date. Part 2 - Carcharhiniformes. 655 p. Rome: FAO.

COX K.W., 1963. - Egg-cases of some elasmobranchs and a cyclostome from Californian waters. *Calif. Fish Game*, 49: 271-289.

CROSS J.N., 1988. - Aspect of the biology of two scyliorhinid sharks, *Apristurus brunneus* and *Parmaturus xaniurus*, from the upper continental slope off southern California. *Fish. Bull.*, 86(4): 691-702.

DULVY N.K. & J.D. REYNOLDS, 1997. - Evolutionary transitions among egg-laying, live-bearing and maternal inputs in sharks and rays. *Proc. R. Soc. Lond. B*, 264: 1309-1315.

GOMES U.L. & M.R. DE CARVALHO, 1995. - Egg capsules of *Schroederichthys tenuis* and *Scyliorhinus haeckelii* (Chondrichthyes, Scyliorhinidae). *Copeia*, 1995(1): 232-236.

HAMLETT W.C. & T.J. KOOB, 1999. - Female reproductive system. *In:* Sharks, Skates, and Rays. The Biology of Elasmobranch Fishes (Hamlett W.C., ed.), pp. 398-443. Baltimore: Johns Hopkins Univ. Press.

MUÑOZ-CHÁPULI R. & A. PEREZ ORTEGA, 1985. - Resurrection of *Galeus atlanticus* (Vaillant, 1888), as a valid species from the NE-Atlantic Ocean and the Mediterranean Sea. *Bull. Mus. natn. Hist. nat.*, Paris, 4e sér., 7, section A, 1: 219-233.

NAKAYA K., 1975. - Taxonomy, comparative anatomy and phylogeny of Japanese catsharks, Scyliorhinidae. *Mem. Fac. Fish. Hokkaido Univ.*, 23: 1-94.

NAKAYA K. & K. SATO, 1998. - Taxonomic review of *Apristurus laurussonii* (Saemundsson, 1922) from the eastern North Atlantic (Elasmobranchii: Scyliorhinidae). *Cybium*, 22(2): 149-157.

NAKAYA K. & M. STEHMANN, 1998. - A new species of deep-water catshark, *Apristurus aphyodes* n. sp., from the eastern North Atlantic (Chondrichthyes: Carcharhiniformes: Scyliorhinidae). *Arch. Fish. Mar. Res.*, 46: 77-90.

POLL M., 1951. - Poissons, I. Généralités, II. Sélaciens et Chimères. *Inst. R. Sci. Nat. Belg., Exped. Océan. Belg. Eaux Côt. Afr. Atlant. Sud (1948-49)*, 4(1): 1-154.

RICHARDSON A.J., MAHARAJ G., COMPAGNO L.J.V., LESLIE R.W., EBERT D.A. and M.J. GIBBONS, 2000. - Abundance, distribution, morphometrics, reproduction and diet of the Isak catshark. *J. Fish Biol.*, 56: 552-576.

SPRINGER S., 1979. - A revision of the catsharks, Family Scyliorhinidae. *NOAA Technical Rep.*, MNFS Circular 422: 1-152.

TORTONESE E., 1956. - Fauna d'Italia. Vol. 2. Leptocardia, Cyclostomata, Selachii. 334 p. Bologna: Edizioni Calderini.

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